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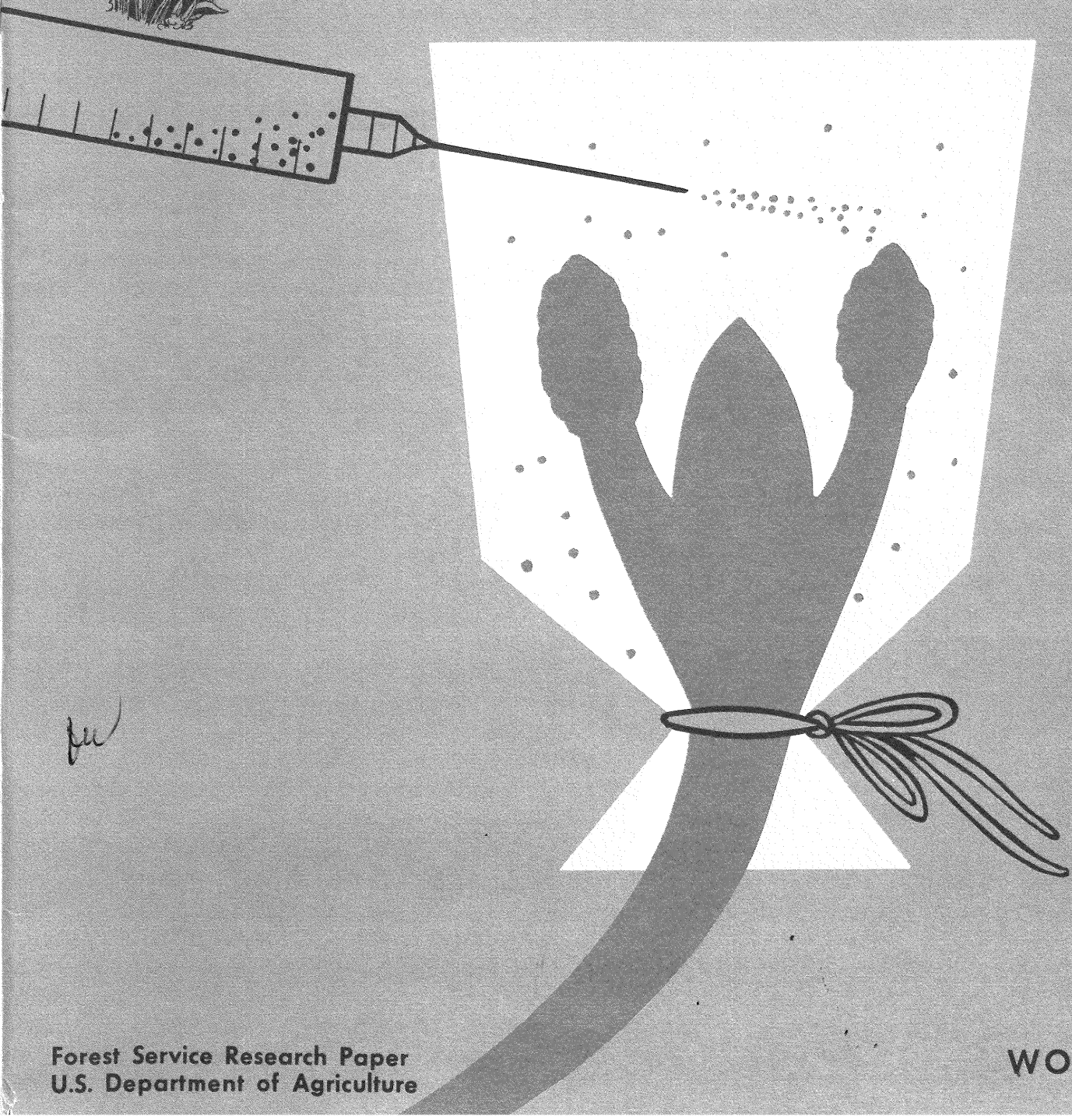
# GENETICS

NOTIFICATION COPY - I&E

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of WHITE SPRUCE



This publication is one in a series on the genetics of important forest trees of North America being published by the Forest Service, U.S. Department of Agriculture, in cooperation with the Society of American Foresters. Development of this series is in accord with the resolutions of the World Consultation on Forest Genetics and Tree Improvement at Stockholm in 1963 and the Second World Consultation on Forest Tree Breeding at Washington, D.C., in 1969. The Committee on Forest Tree Improvement of the Society of American Foresters undertook the preparation of manuscripts for North American species.

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## SUMMARY ABSTRACT

The review covers more than 100 references and some unpublished information.

The evolution, migrational history, and distribution of *Picea glauca* (Moench) Voss as it is currently understood is briefly discussed.

White spruce reaches sexual maturity relatively late, but early prolific seed production in grafted seed orchards appears to be possible. The review summarizes the phenology of generative bud development, pollination, fertilization, and seed maturation. In the species, selfing ability apparently is a genotypic characteristic with some trees self-fertile. Controlled pollination techniques and pollen extraction and storage are described as well as the establishment of experimental plant material from seed.

Vegetative propagation is best accomplished by grafting, and some common techniques are described, but white spruce is considered a hard-to-root species.

The growth rate is compared to that of other north temperate species. It is one of the most radiosensitive species tested, perhaps due to its large nuclear size and high DNA content. Interspecific hybridization in nature among *P. glauca* and *sitchensis* and *engelmannii* is common with introgressed populations covering wide regions. Natural hybridization with *P. mariana* occurs rarely. The attempts to cross the species artificially are summarized; some of the crosses are of promise due to hybrid vigor.

Provenances show a wide range of variation in characteristics such as: (1) height growth, (2) some needle characteristics, (3) wood density, (4) insect resistance, (5) nuclear volume, (6) leaf oil terpenes, (7) response to calcium ion concentration, and (8) germination temperatures. Provenances from southeastern Ontario have been tested in a wide range of

environments and have grown well in most of them.

Genetic variation within provenances in height growth is considerable and it should be possible to select simultaneously for fast growth and late flushing, which is related to reduced frost injury. Other inherited characteristics of the individuals are: (1) pollen radiosensitivity, (2) fruitfulness, and (3) peroxidase and esterase isoenzyme content.

Cytogenetic information is limited.  $2n = 24$ . Polyploids are rare and they are stunted.

Potential benefits possible by the production and use of improved strains of white spruce are far in excess of the cost of the required research and development. Genetic variability is wide and many options are open to the breeder: (1) selection of superior provenances, (2) hybridization of provenances, (3) selection of superior individuals within provenances for random or particular crosses, and (4) species hybridization. These options are briefly discussed.

Past provenance research has been based on too few samples and new studies covering the entire range of the species are needed. Another high priority area of research is provenance hybridization.

Needed biometric data include correlations between juvenile and mature characteristics, character correlations, and genetic parameters. The components of yield and pest and disease resistance are not now known. Research is needed on seed orchard designs and, although perhaps of lower priority, studies of species hybridization should be continued.

Many basic problems need study — DNA variation and base composition, isoenzymes, monoterpenes, maternal inheritance, and others.

# The Genetics of White Spruce

Hans Nienstaedt<sup>1</sup> and Abraham Teich<sup>2</sup>

## INTRODUCTION

White spruce, *Picea glauca* (Moench) Voss, is one of the most widely distributed conifers in North America. It has a considerable growth potential and produces a high-grade pulp, preferred in the production of quality paper. By far the greatest use of spruce is for pulpwood, but other uses include lumber of all kinds, specialties such as sounding boards, paddles and oars; and most recently an increasing use for veneer. It has, therefore, been planted extensively during the past 30 years in north-central

and northeastern United States and in the adjacent Canadian provinces.

Research on the genetic variation of the species, which began during the 30's in both Canada and the United States, has shown that it is a highly variable species with a great potential for genetic improvement.

The purpose of this paper is to review the current status of research, to point out new potentially fruitful areas of research, and to suggest directions for developmental tree improvement programs.

## EVOLUTION, MIGRATIONAL HISTORY, AND DISTRIBUTION

*Picea* probably originated in northeastern Asia (Wright, 1955) and perhaps reached North America through more than one wave of migration (Wright, 1955; Gordon, 1968; Hills and Ogilvie, 1970). Basing his interpretation on species cross-compatibilities and taxonomic affinities, Wright suggested that the *P. rubens-mariana* group of eastern America is more ancient than the *P. glauca-engelmannii-pungens-sitchensis* group of the Northwest. He considered *P. jezoensis* (Sieb. and Zucc.) Carr. to be the link between the Asiatic and the northwestern American spruce species. More recently, Fowler (1966), on the basis of new crossability studies, suggested that *P. glauca* and not *P. jezoensis* is the connecting link between the Asiatic and North American spruces. The recent find of fossil cones of an extinct species, *Picea banksii*, may support Fowler's hypothesis. The fossils were found on Banks

Island in Arctic Canada, associated with a formation from the late Miocene or early Pliocene. *P. banksii* has cones similar to *P. rubens* Sarg., *P. mariana* (Mill.) B.S.P. and *P. glauca*, and can only be differentiated from *glauca* on the basis of mean cone size (Hills and Ogilvie, 1970). Hills and Ogilvie, on this evidence, conclude that *P. glauca*, or a close ancestor such as *P. banksii*, provided the link between North American and Asiatic species of spruce and not *P. jezoensis*. They state that "the *P. glauca-engelmannii-pungens-sitchensis* group originated through *P. banksii*, from which *P. glauca* developed and subsequently the relatively recent *sitchensis-engelmannii-pungens* complex became differentiated." They suggest that the *mariana-rubens* group is related to the basal *glauca* line preceding the origin of *P. banksii*. Fowler<sup>3</sup> has questioned this interpretation of the origin of the *mariana-rubens* group and suggests that the separation from the *glauca* line goes back at least to *omorika*. He also suggests that the group reached North America

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<sup>3</sup> Fowler, D. P. Canadian Forestry Service, Fredericton, New Brunswick. Personal communication, January 1971.



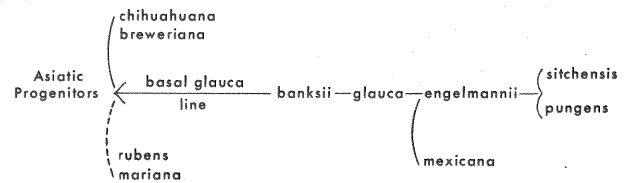
from the east during the Cretaceous prior to continent separations.

An acceptable hypothesis on the evolution of the American spruces must account for the origins of three relict species: *P. chihuahuana* Martinez, *P. mexicana* Martinez, and *P. breweriana* S. Watson. *P. mexicana* is a recently described species discovered in 1961. In Dallimore and Jackson (1967) it is considered "intermediate in some respects" between *P. engelmannii* Parry and *P. pungens* Engelm., and considering the cone characteristics it is undoubtedly correct to place it close to the *P. glauca-engelmannii-pungens-stichensis* group. Wright's (1955) taxonomic analysis places *P. breweriana* and *P. chihuahuana* close to each other, and he points out their similarity to some of the southern species in China. He concludes that they "almost certainly" are of different stock than the species of northwest America. Gordon (1968) places the origin of *P. chihuahuana* as early as Cretaceous or even Jurassic. As an alternative, he suggests an early Tertiary (Eocene) entry of *P. chihuahuana* or a progenitor with a southward advance during the cooler Miocene. The *P. banksii* and the *P. chihuahuana* cones are similar;<sup>4</sup> *P. banksii* is late Miocene or early Pliocene. Hills and Ogilvie (1970) suggested that *P. mariana* and *P. rubens* are related to the basal *glauca* line, perhaps *P. chihuahuana* and *P. breweriana* are ancient species related to the same basal line and to *P. banksii*. Certainly, the suggested age and the similarity in cone morphology do not contradict such a conclusion.

No complete review of all fossil spruce records dating back through the Pleistocene and Tertiary to the Cretaceous epochs has been found. Such a review and additional studies of cross-compatibility of the North American spruces will be required before a complete hypothesis of North American spruce evolution can be formulated. An interim working hypothesis based on the material reviewed here is shown in next column.

*Picea glauca* has spread over a larger part of North America than any other coniferous tree species (Wright, 1956)—a reflection of its con-

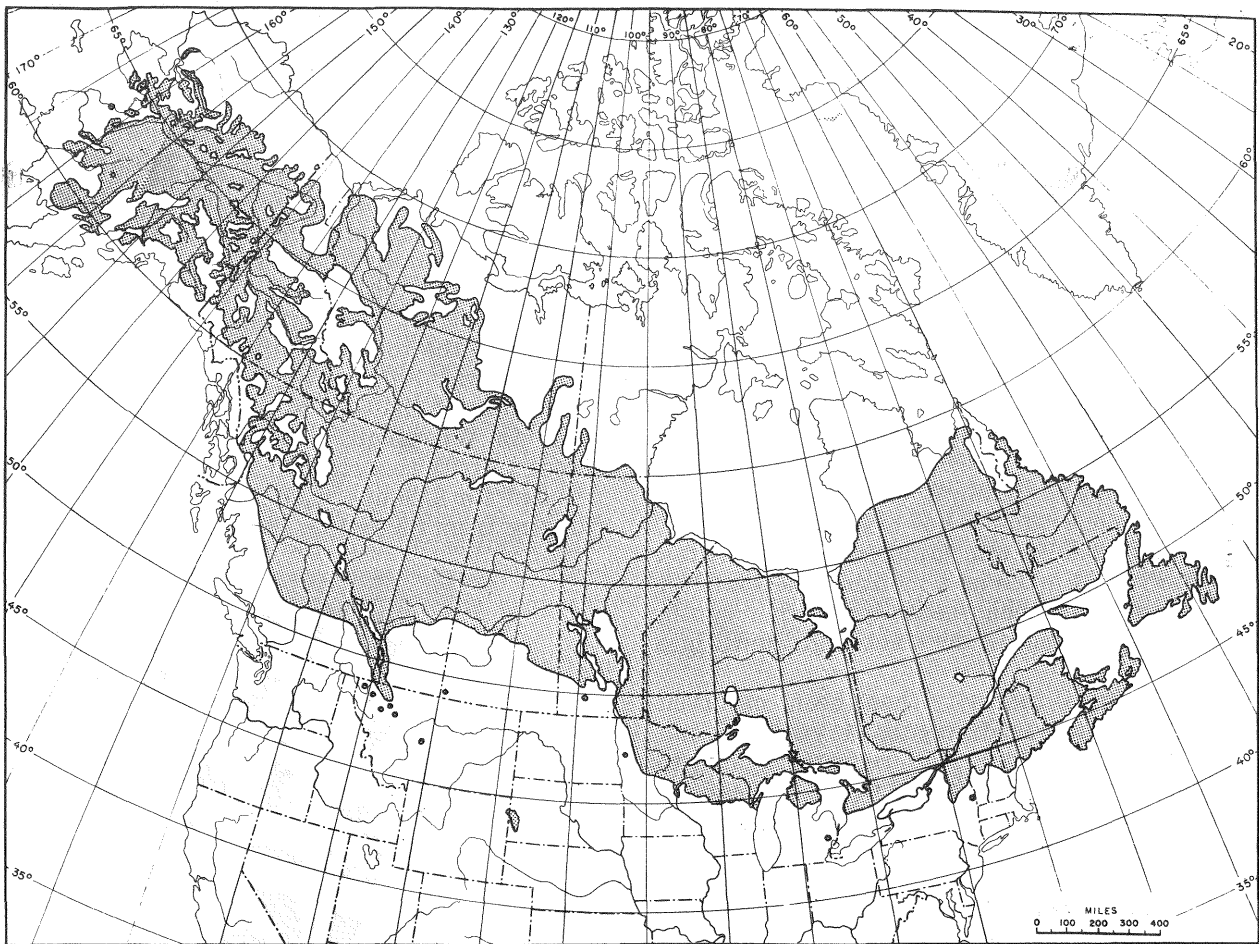
The Possible Phylogeny of North American  
*Picea* Species



siderable genetic variation. Several distribution maps are available (Nienstaedt, 1957; Fowells, 1965; Sutton, 1969), but detailed maps are lacking in the literature. Fowell's map is shown in figure 1. Pollen studies support past distribution, during the Climatic and Little Climatic Optima—3500 and 900 years ago—"at least 280 Km north of the forest of which white spruce is currently a component."

During late glacial times, spruce forests, with white spruce as a major component, dominated the landscape from the Great Plains (Watts and Wright, 1966; Ritchie, 1966) to New England until the pronounced climatic change about 11,000 years ago when it retreated rapidly to the north (Wright, 1968). The distribution of white spruce may have reached as far south as Lee County, Texas (Pötzger and Tharp, 1943; Graham and Heimsch, 1960) and North Carolina (Frey, 1951). According to Watts and Wright (1966), the forests in the "western mountains" (apparently they refer to the entire mountain system) descended to lower altitudes with the result that "the conifers from Canada" (presumably eastern Canada and northern U.S.A.) and from the eastern Rockies probably were in contact in the western Great Plains during the Wisconsin glaciation. Löve (1959) suggested a reserve of northern conifers (and northern deciduous trees) existing close to the foot of the Rocky Mountains, and Halliday and Brown (1943) postulated that both white and black spruce survived the Illinoian and Wisconsin glaciation in refugia south of the ice, in the unglaciated Yukon Valley, and perhaps along the exposed Atlantic continental shelf. Löve (1959) also mentioned the possibility that the refugia in Yukon-Alaska and the lower eastern slopes of Rocky Mountains were joined during the Wisconsin glaciation "by a fluctuating corridor" through Alberta.

<sup>4</sup> Data on file, Institute of Forest Genetics, NCFES, USDA, Forest Service, Rhinelander, Wisconsin.



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Figure 1.—The botanical range of white spruce (Fowells' Map, 1965).

## SEXUAL REPRODUCTION

### Reproductive Development

Primordia of strobili are laid down in late July or early August (Fraser, 1962; Eis, 1967). According to Eis (1967), generative activity at the bud apex begins approximately when elongation growth ceases, which is about late July. Shortly after mid-August, male buds develop microsporangia with rudimentary pollen sacs, and female buds produce bract and ovuliferous scale primordia. Primordia of male and female reproductive strobili continue to grow throughout the fall and into winter. Rauter and Farrar (1969) observed that the fall activity consists of cell expansion rather than cell division. By February the outline of the ovules can be recognized with no apparent tissue

differentiation. Each lateral extension of ovuliferous scales bears a single ovule. In the male bud, the archesporia are present within the microsporangium. Meiosis begins after a critical temperature is reached in the spring and pollen shedding follows after approximately 3 weeks (Winton, 1964a). Pollen shedding and female maximum receptivity usually occur simultaneously for 3 to 5 days in May, June, or July, depending upon geographic location and climate (Wright, 1953a; Nienstaedt, 1958; Sutton, 1969). On the coast of James Bay north of 53°N, it is as late as July 12 (Hustich, 1950). Fertilization takes place approximately 3 weeks after pollination (Rauter and Farrar, 1969). Male strobili are red or pale red, while female strobili are red, pink, or green. Female flower

color is possibly under the control of a gene with two non-dominant alleles (Teich, 1970a).

At Indian Head, Saskatchewan natural seed dispersal occurred about 98 days after pollen anthesis, but the seed reached maximum size and viability about 2 weeks earlier. Seeds shed naturally when the cone specific gravity reaches 0.744 or the moisture content reaches 48 percent. To obtain maximum seed viability, it is recommended that cones not be collected more than 1 week before natural seed shed (Cram and Worden, 1957). At Riding Mountain Forest, Manitoba (50°N, 100°W), Waldron (1965) observed an average initiation of seedfall in early August building up to a peak in late August or early September. Dissemination is about 90 percent complete within 5 weeks of cone opening and is more rapid in hot weather. In several years with cool or wet summers, peak seedfall was delayed as much as a month. The soundest seed fell during peak seedfall. Further south, in Wisconsin, seedfall does not begin until late in August.

Reproductive maturity has been observed in white spruce as young as 4 years Sutton (1969); and Wright (1964) reported moderate numbers of cones on some 6- to 10-year-old trees, and cones in quantity on 10- to 15-year-old white spruce. Nienstaedt and Jeffers (1970), however, found that moderate cone crops are not produced in northeastern Wisconsin until the trees are older. For example, in a heavy seed year, due to absence of flowers, only 10 out of 23 trees 21 years old could be included in a pollination program requiring a minimum of 10 pollination bags per tree. Other references indicate that trees are generally 30 or more years old before they produce seed in quantity (Stiell, 1955; USDA Forest Service, 1948), and the early production reported by Wright (1964) probably is an exception.

Nienstaedt and Jeffers (1970) found that, on the average, grafts from sexually mature trees produce as many as 45 cones 6 years after grafting (fig. 2); cone yield increased fourfold by the time the grafts were 9 years old. Clonal seed orchards may, therefore, be the preferred breeding system for white spruce if an early yield of improved seed is desired.

Total yield of 271,000 viable seed in one season from an individual tree has been estimated (Roe, 1952), and a mature stand in Manitoba (50°N, 100°W) produced 3,300,000 seed per acre in a good seed year and averaged 670,000 sound seed per acre per year over a 10-year period (Waldron, 1965). Considering that Holst

*et al.* (1969) reported as many as 4700 cones in an isolation tent covering the crown of a mature tree, these per-acre yields seem low for a stand with about 100 dominant or co-dominant trees per acre.

Variation in yield of seed among individual trees has been reported by a number of workers and is clearly a characteristic of the genotype. Whether provenances differ in such yield is not known; most likely they do. Tripp and Hedlin (1956) reported that at an unstated location in Canada the total potential number of seeds per cone was 140, but only the central 66 percent or less of the cone actually produced viable seed. In Wisconsin, King, Jeffers, and Nienstaedt (1970) reported an average of 91 seeds per cone for 8 clones, with the average per clone ranging from 59 to 109. Rudolph (1969) found

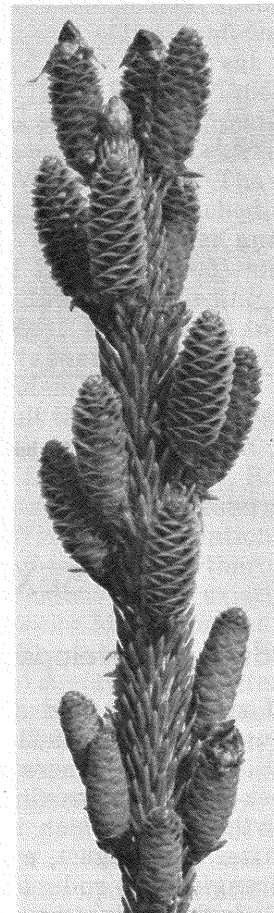


Figure 2.—Profuse female strobili production on a 6-year-old white spruce graft. The strobili in the center and top are in the latest stages of receptivity, while the lower ones already have closed.



74, 82, and 87 total seeds per cone in three different trees. Commonly, the average number of filled seed per cone is less than these values, ranging from 23 (Tripp and Hedlin, 1956) to 34.<sup>4</sup>

In years with light cone crops, little or no sound seed is found in the cones (Tripp and Hedlin, 1956). The number of viable seed will vary depending on the weather condition during pollination, fertilization, and seed development; Nienstaedt (1958) found only 6 filled seeds per cone in a year when pollination occurred during unfavorable weather.

At sexual maturity, heavy cone crops are produced only every 2 to 6 years with light crops in between (Fowells, 1965). This in part stems from the fact that strobili are formed in lateral buds that would otherwise form vegetative shoots. The crown must regenerate short branchlets before a new heavy cone crop can be produced.

Purely male and purely female strobili are usually formed on the same tree, but occasionally male and female structures are found within the same conelets. The formation of bi-sexual cones is believed to be induced by drought (Santamour, 1959).

### Cross- and Self-pollination

Cross-fertilization is normal in stands of white spruce and the extent to which self-fertilization takes place under natural conditions is not known.

Within the crown of an individual tree, pollen-shedding and maximum female receptivity coincide (Nienstaedt, 1958; Wright, 1953b). There is a general separation of female and male strobili with the females concentrated in the top quarter of the crown, but the zone of overlap is usually great and it is doubtful that the vertical distribution of the sexual structures is an effective barrier to self-fertilization.

Seed-set resulting from controlled self-pollination is characteristic of the individual genotype (Fig. 3). Of 18 trees (or clones) studied at Rhinelander, Wisconsin, 7 produced less than 5 percent full speed per cone (i.e., 3 to 5 full seeds per cone), 3 produced between 5 and 10 percent, 4 between 10 and 20 percent, and 4 trees more than 20 percent filled seed. All were pollinated in the same season, and we do not know if the ability of a particular genotype to set self seed varies from year to year. There is some evidence that the more self-fertile trees also are the most fertile when out-crossed (King, Jeffers, and Nienstaedt, 1970).<sup>4</sup>

King, Jeffers, and Nienstaedt (1970) studied the effect on seed yield and seed quality of various proportions of self-pollen during pollination and found no evidence of discrimination against self-pollen. They used pollen mixtures containing 0, 12, 50, 90 and 100 percent self-pollen and found that seed yield varied in direct proportion to the amount of self-pollen in the mixture. Also, the measured epicotyl growth compared closely to the value predicted assuming that no discrimination against self-pollen had occurred.

Therefore, even when in direct competition, outcross pollen has no advantage over self-pollen prior to fertilization, and in white spruce self-sterility is not caused by a failure of self-fertilization (Navasajtis, 1966). Most of the embryos fail to develop (Klaehn and Wheeler, 1961; Mergen, Burley, and Furnival, 1965), probably as a result of homozygous lethal recessive loci (King, Jeffers, and Nienstaedt, 1970).

### Controlled Pollination Techniques

Controlled pollination in the southern part of the species range in Wisconsin and Ontario is usually done in the last 2 weeks in May and the first week of June. In northeastern Wisconsin, it has been performed as early as May 13 and as late as June 3.

Bagging should precede pollination by about 1 week, when the female strobili usually are deep purple in color (some remain green or pink), breaking through the bud scales, and becoming erect. At earlier stages female buds can be recognized by their longer, narrower, more pointed shape (Nienstaedt, 1958).

Various bagging materials have been used. Clear sausage casing alone is not satisfactory, but when covered with a kraft paper bag gives good results. Pollination bags of non-woven fiber are also satisfactory and framed cloth tents (Fig. 4) designed to facilitate large-scale pollination have been described (Yeatman, 1959; Roche, 1969a). Such individual isolation tents on white spruce have yielded from 1400 to 4700 cones (Holst, *et al.*, 1969), but the yield of filled seed was disappointingly low (Yeatman, 1971).

White spruce pollen is easy to collect by removing small branches from the parent trees when the male strobili are about 10 to 12 mm long and nearly dry when squeezed. The branches are placed on sheets of paper in low humidity at room temperature. The male strobili will then release the pollen in 24 to 48 hours.



Figure 3.—Selfing in white spruce results in severe inbreeding depression. The selfed plot in the foreground (black arrows) showed 25 percent mortality and an average height of the living trees of .95 m. In the wind-pollinated progeny (white arrows) there was no mortality and the average height was 1.88 m. Planted May 1963 with 2-2 stock. Photo August 1970.

Male strobili can be forced on large branches brought into the greenhouse and placed in water in late January. During January, February, and March, 3 to 4 weeks forcing is required for pollen shedding (Winton, 1965).

Pollen can easily be stored for up to 1 year without dessication at 0° to 3°C in closed containers. Razmologov (1964) reported 76.5 percent germination after 14 months of storage at 4°-5°C and 40 percent relative humidity. Vacuum dried pollen stores well for as much as 1 year (Barber and Stewart, 1957), and vacuum dried pollen stored at either room temperature or -20°C produced comparable seed yields (Feret and Stairs, 1970). Winton (1965) tested germination with 5 percent dextrose at 21° to 27°C; 50 to 60 hours incubation was required. Razmologov (1964) obtained the best results using 5 percent sucrose in a 0.8 percent agar solution. Reports of longer storage are lacking, although one case of storage for 11 years at -18°C in a dessicator is on record. This pollen germinated 70 percent in a 10 percent sucrose solution, but yielded only 3 percent viable seed in controlled pollinations.<sup>5</sup>

## Seed Germination and Establishment

Maximum germination of valuable seed can be assured without stratification by germinating it on the surface of a medium such as perlite in covered dishes, with 18- to 20-hour photo-periods. After seed has imbibed distilled water for 2 hours, a single exposure to light for 20 hours also assured prompt germination (Phipps, 1969). After the combined length of radicals and hypocotyls have reached 1 to 2 cm, the seedlings can be planted in soil.

Covered in soil, freshly harvested white spruce seed germinates best following 4 weeks stratification at 1° to 3°C. Germination begins about 10 days after sowing and is almost complete by the twenty-third day (Santon, 1970). Stratification for 60 to 90 days at 5°C in moist sand is recommended for stored seed (USDA, Forest Service, 1948), but may in some cases reduce the germination percent (Hellum, 1968).

<sup>5</sup> Yeatman, C. W. Data on file Petawawa Forest Experiment Station, Chalk River, Ontario.



Figure. 4.—Reciprocal (diallel) crossing in white spruce using tree crown isolation tents and small isolation bags. Photo courtesy of Petawawa Forest Experiment Station, Ontario.

## VEGATATIVE PROPAGATION

### Grafting

Consistently successful grafting of white spruce can be achieved by using 8 to 10 cm scions of current growth on well established 4- to 5-year-old white or Norway spruce (*P. abies* (L.) Karst) rootstock. For greenhouse grafting, the rootstocks should be potted in the late spring prior to grafting. After seasonal growth is completed, the rootstock requires chilling out-of-doors until the latter part of December or for about 8 weeks in the coldroom at about 2°C (Nienstaedt, 1966). Forced in the greenhouse, root activity begins in 2 to 3 weeks and stock plants are then ready to graft. Subsequent growth of the scions is improved when the grafts are maintained on 18- to 20-hours photoperiod.

The side-veneer graft gives excellent results;

scions from old mature spruce should be grafted in a dominant position on the rootstock and the lower branches on the stock plant maintained until the graft is at least 3 to 4 years old and starts rapid growth. In this dominant position even scions from very old trees will overcome the branch habit that is the common result of grafting low on the rootstock (Holst, *et al.*, 1969).

Grafting in the field can be equally successful; trees in 5- to 7-year-old plantations can be worked conveniently. In northern Wisconsin grafting is best done about May 1, just when the vegetative buds begin to swell. Side veneer grafts placed low on last year's leader are usually the most successful.

While winter grafting in the greenhouse and spring grafting in the field are the most reliable, grafting can be done during a 2-week

period in the latter part of July in the field as soon as leader growth is completed and the scions are partially lignified (Nienstaedt, 1965). Successful grafting in the middle of September in the greenhouse also has been described in detail by Nienstaedt (1959).

### Rooting of Cuttings

Farrar and Grace (1940) reported that 80 to 90 percent of cuttings collected in late July on 10- to 15-year-old trees rooted. Rauter (1971) rooted cuttings from 3-year-old seedlings with 60 to 90 percent success. She compared the ability to root of different populations and of different individuals within the populations and observed variation at both levels. The ability to root decreases rapidly with age. Girouard (1970) took cuttings in

June; after 15 or 16 weeks, 45 to 58 percent of those taken from 7-year-old trees had rooted, while only 13 to 23 percent of the cuttings from 19-year-old trees had done so. The rooting of cuttings from old trees can be somewhat improved if the scions are first grafted on vigorous young rootstock. Ten to twenty percent of the cuttings from ramets of about 100-year-old ortets and 16 percent of those from a 180-year-old ortet rooted (Holst, *et al.*, 1969).

Using 9- to 12-year-old trees near East Lansing, Michigan, Feucht, Watson, and O'Rourke (1961) obtained 12 to 18 percent rooting after 100 days from air-layers. Growth regulating chemicals had no beneficial effect. They also found that air-layers placed on the trees May 1 gave the highest percentage rooting, while the greatest root length developed on June 1 air-layers.

## GENETICS AND BREEDING

### Species Comparisons

The rate of height growth of white spruce has been compared with other species, but in most cases the comparisons have been highly dependent upon the environments in which the growth was studied and the seed source of the species tested. Growth has been compared with Norway spruce in many field experiments in eastern Canada and northeastern United States (Stiell, 1958; Holst, 1963; MacArthur, 1964; King and Rudolf, 1969; Teich and Morgestern, 1969). In many experimental plantings close to the coast, Norway spruce has grown more rapidly than white spruce, while in inland experiments white spruce has grown as rapidly as or more rapidly than Norway spruce. Available moisture and humidity are apparently key factors (Holst, 1963).

Where several provenances of each species were compared, provenance appeared to be a more important criterion than species, and genotype (provenance)  $\times$  environment interaction becomes important. In a 20-year-old test in northeastern Wisconsin, white spruce from Douglas (45.5°W Lat. and 76.9°N Long.) and Angus (44.2°W Lat. and 75.9°N Long.), Ontario, outgrew all six Norway spruce provenances tested (Holst, 1963). At 33 years from seed, the growth of white spruce provenances from Douglas, Ontario; Chippewa National Forest, Minnesota; and Port Arthur, Ontario, exceeded the six Norway spruce seed sources;

the Angus white spruce was fifth of seven white spruces but still exceeded four of the six Norway spruce provenances. The most rapidly growing Norway spruce still outgrew four out of seven white spruce provenances. In a test of the same material in a different environment on the Superior National Forest in northeastern Minnesota, Norway spruce provenances were generally faster growing than white spruce provenances, but the most rapid growing white spruce provenance grew as rapidly or more rapidly than four out of the six Norway spruce provenances tested (King and Rudolf, 1969).

In most published comparisons of white spruce with other species, provenance variation and differential response to environmental factors are ignored. Van den Driessche (1968) found that low light intensity favored white spruce compared to black spruce, balsam fir (*Abies balsamea* (L.) Mill.) and eastern white-cedar (*Thuja occidentalis* L.). Logan (1969) also found that at low light intensity white spruce stems grew faster than the other 3 species. The stems at 9 years of age were 3.9, 2.2, and 1.7 times heavier than black spruce, balsam fir, and white-cedar respectively. At full light intensity the stems were still 2.9 times heavier than balsam fir, but lighter than black spruce and white-cedar stems by factors of 0.34 and 0.95 respectively.

Of the gymnosperm species tested in some detail, white spruce is one of the most sensitive to gamma radiation. The mean inhibitory seed



exposures determined from eight seedling development endpoints were 2.30, 3.23 and 4.84 kR<sup>6</sup> for *P. abies*, *P. glauca* and *P. mariana* respectively. For *Pinus banksiana* Lamb.—the most resistant gymnosperm tested—the comparable mean inhibitory exposure was 9.71 kR (Rudolph and Miksche, 1970). When seedlings rather than seed are exposed, inhibitory exposures are much lower. One study of four seedling characteristics found 50 percent inhibition at 0.40 and 0.51 kR in *P. glauca* and *P. mariana* respectively (Rudolph, 1971, 1971b). Lethal gamma radiation exposures for pollen as determined from seed yield and quality analysis are much higher than for seed and seedlings and probably approximate 20 kR to 30 kR (Stairs and Troendle, 1969; Rudolph, 1969, 1971b). The 50 percent lethal exposures varied between 5.3 kR and 9.7 kR in three trees, depending upon the endpoint used (Rudolph, 1971b). Inconclusive data by Stairs and Troendle (1969) suggest that *P. abies* pollen is more sensitive than that of *P. glauca*.

### Interspecific Hybrids

In regions where *P. glauca* and *P. sitchensis* (Bong.) Carr. are sympatric, natural hybridization occurs. A natural hybrid has been described as *P. x lutzii* Little on the basis of specimens collected on Kenai Peninsula, Alaska (Little, 1953), and the introgressed populations of spruce in the Skeena River Region of British Columbia have been described in detail by Garman (1957), Daubenmire (1968), and Roche (1969b). Hanover and Wilkinson (1970) studied needle samples from the same region and demonstrated the usefulness of chromatographic studies of the phenolic compounds in distinguishing between the parent species and their hybrid.

Introgressive hybridization is widespread where *P. glauca* and *P. engelmannii* are sympatric over large parts of British Columbia, Alberta, and Montana. In Alberta, typical white spruce is largely confined to the warmer, drier valleys below 5,000 feet, and Engelmann spruce to the cooler, more moist conditions above 6,000 feet. A hybrid swarm occupies the intervening slopes (Horton, 1959). Taylor (1959), on the basis of studies of limited samples, concluded that *P. glauca* and *P. engelmannii* are subspecies of a single species.

Roche (1969b), from his extensive study of the complex, concludes that "the pure forms of white and Engelmann spruce in British Columbia are distinct taxonomically and occupy quite distinct ecological niches." Horton (1959) considered them distinct species; La Roi and Dugle (1968) concluded that the specific status of the two species probably should be maintained. The authors of this review share this viewpoint, and suggest that in addition to the genecological and systematic studies outlined by La Roi and Dugle (1968), a comprehensive review of fossil spruce records in North America may help clarify the relationship between *P. glauca* and *P. engelmannii*.

Roche (1969b) also describes possible introgressive hybridization between *P. glauca* and *P. mariana* in British Columbia, but in the eastern parts of their overlapping ranges few natural hybrids have been reported (Little and Pauley, 1958; Larsen, 1965).

Cone scale morphology has been the best basis for distinguishing between the species and their introgressed products (Horton, 1959; Roche, 1969b; Taylor, 1959). But more recently, chemosystematic techniques have found wide use in studies of natural hybridization between *P. glauca* and *P. sitchensis* (Hanover and Wilkinson, 1970); *P. glauca* and *P. engelmannii* (La Roi and Dugle, 1968; Ogilvie and von Rudloff, 1968; and Habeck and Weaver, 1969); and *P. glauca* and *P. mariana* (von Rudloff and Holst, 1968).

To illustrate the leaf oil composition and the use of the technique, the results by Ogilvie and von Rudloff (1968) are shown in table 1. The data are based on material collected along the Bow River in Alberta. The Boreal and Tree-line population illustrate "pure" white and Engelmann spruce, respectively. Foothill, Lower Valley, and Midvalley populations, on the basis of morphological characteristics, are *glauca* or *glauca*-intermediate types, while the Upper Valley population is intermediate between the two pure species.

Species cross-compatibility studies have involved white spruce and about two-thirds of the other species in the genus. The following compilation summarizes the results. Of necessity, it is a summary of already published summaries. The data available are not always comparable and the four classes used in the lists are, therefore, subjective both with regard to the success of the crosses and the verification of hybridity.

<sup>6</sup> 1 kR = 1000 roentgens



### Successful crosses; hybridity verified

<i>P. engelmannii</i>	Wright, 1955
<i>P. jezoensis</i> var. <i>hondoensis</i> (Mayr.) Rehder.	Wright, 1955
<i>P. koyamai</i> Shirasawa	Wright, 1955
<i>P. sitchensis</i>	Wright, 1955
<i>P. omorika</i> (Pancic)	Jeffers, 1971
Purkyne	
<i>P. pungens</i>	Hanover and Wilkinson, 1969
<i>P. schrenkiana</i> Fisch. & Mey.	Fowler, 1966

### Crosses of limited success; hybridity verified

<i>P. maximowiczii</i> Reg.	Jeffers, 1971
<i>P. smithiana</i> Boiss.	Mergen, Burley and Furnival, 1965
<i>P. likiangensis</i> (Franch.) Pritz.	Jeffers, 1971

### Possible crosses of limited success; hybridity not verified

<i>P. asperata</i> Mast.	Mergen, Burley, and Furnival, 1965
<i>P. orientalis</i> (L.) Link	Mergen, Burley, and Furnival, 1965
<i>P. retroflexa</i> Mast.	Jeffers, 1971
<i>P. montigena</i> Mast.	Jeffers, 1971
<i>P. abies</i>	Jeffers, 1971
<i>P. mariana</i>	Wright, 1955
<i>P. glehnii</i> (Fr. Schmidt) Mast.	Anonymous, 1962

### Crosses that have failed

<i>P. rubens</i>	Wright, 1955, 1962; Jeffers, 1971; Anonymous 1962; Fowler, et al., 1971.
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*P. balfouriana* Reh. & Wright, 1955

Wilson

*P. wilsonii* Mast. Wright, 1955

Hybrid vigor has been reported for some of

the crosses. *P. sitchensis* x *P. glauca* (*P. lutzii*) grew at the parental rates but *P. glauca* x *P. engelmannii* and *P. glauca* x *P. jezoensis* demonstrated considerable hybrid vigor (Wright, 1962). *P. schrenkiana* x *P. glauca* was 20 percent taller than *P. schrenkiana* and 50 percent taller than *P. glauca* at 22 weeks of age (Fowler, 1966). Hybrid vigor in crosses *P. glauca* x *P. pungens* has also been reported. Santamour (1967) found that the hybrid exceeded the tallest parent (*P. glauca*) by 21.5 percent at 9 years from seed, while Hanover and Wilkinson (1969) found a 9.6 percent height advantage at 13 weeks.

Seedlings of the cross between *P. omorika* and *P. glauca* exceeded white spruce by 40 percent after they were forced in the greenhouse and grown in the nursery for 1 year. Compared to *P. omorika*, the hybrids show little injury from fall frost or winter cold (Jeffers, 1971).

It is difficult to exploit most of the reported interspecific hybrid vigor because seed-set is low. However, Wright (1962) suggested that, in the case of *P. glauca* x *P. jezoensis*, large quantities of seed can be produced cheaply on

Table 1.—Mean percentage composition of spruce leaf oils from the Bow River area as compared with boreal white spruce (from Ogilvie and von Rudloff, 1968)

Peak no.	Boreal 1500'–1800'	Foot-hill 4100'	Lower valley 4250'	Mid-valley 4800'	Upper valley 5100'	Tree-line 7200'
8 $\alpha$ -Pinene	5.9	5.7	4.1	4.6	5.3	4.5
10 Camphene	6.9	5.4	5.8	6.4	6.1	5.9
11 $\beta$ -Pinene	2.0	1.3	2.2	2.1	2.8	3.2
13 Myrcene	5.6	7.8	3.5	8.5	11.1	19.2
14 3-Carene	0.2	0.3	0.1	0.3	3.4	4.1
16 p-Cymene	Trace	Trace	Trace	Trace	0.2	0.1
17 Limonene	12.9	14.2	13.4	9.6	7.3	4.4
18 $\beta$ -Phellandrene	0.9	1.1	0.7	0.8	2.3	6.0
20 Terpinolene	0.5	0.1	0.3	0.7	0.9	0.4
21 1,8-Cineole	0.1	0.2	0.35	0.8	2.1	1.5
23 Unidentified			0.1	Trace	Trace	Trace
25 Unidentified	0.1	Trace	0.1	0.1	0.1	0.1
27 Linalool	Trace	0.1	0.1	0.2	0.6	0.5
31 Camphor	46.5	44.3	51.6	48.3	34.3	28.6
32 Camphene hydrate	0.4	0.6	0.8	0.6	1.0	2.5
33 4-Terpinenol	0.2	0.1	0.3	0.8	1.0	0.5
34 Isoborneol	0.1	Trace	Trace	0.1	0.1	0.1
35 Borneol	1.1	0.8	1.0	1.7	2.5	1.9
36 $\alpha$ -Terpineol	0.7	0.6	0.6	1.2	1.3	1.0
37 Alcohol II	0.2	0.2	0.1	0.1	0.3	0.5
39 Piperitone	0.6	0.4	0.7	1.0	2.3	5.2
41 Bornyl acetate	11.4	12.5	11.5	9.3	7.5	6.4
43 Citronellyl acetate	Trace	Trace	0.1	Trace	Trace	0.6
44 Geranyl acetate	0.1	Trace	Trace	0.2	0.5	Trace
55 $\delta$ -Cadinene	0.5	0.2	0.2	0.8	1.5	0.6
61 Unidentified	0.1	0.1	0.1	0.1	0.6	0.2
62 Unidentified	0.1	0.1	0.1	0.2	1.0	0.3
63 Unidentified	0.3	0.2	0.2	0.3	2.4	0.5

some 20-foot-tall white spruce that produce many seeds per tree but bear no pollen. In one day a man can pollinate sufficient strobili to produce 50,000 to 100,000 seeds on isolated trees without bagging. Also, *P. omorika* x *P. glauca* yields sufficient seed to make artificial hybridization worthwhile, but bagging would be required.<sup>7</sup>

## Genetic Variation Among Provenances

Provenances vary in rate of height growth (Genys, 1965; Holst, 1960, 1962; Nienstaedt, 1969), wood density (Holst, 1960, 1962), branch angle (Holst, 1962), response to soil calcium ion concentration and high nutrient levels (Farrar and Nicholson, 1967; Cunningham, 1971), germination temperature thresholds (Fraser, 1971), nuclear volumes and DNA content (Miksche, 1968) and needle, branch, and bud characteristics.

A summary of the variation in 36 seedling characteristics among 28 provenances representing the entire range of the species is presented in table 2. Simple and multiple regressions were determined using seed weight, latitude, average July temperatures, average January temperatures, precipitation, and growing season as the provenance origin as the independent variables. In spite of the widely scat-

<sup>7</sup> This statement is questionable. More recent research indicates that only certain individuals of the two species are cross-compatible.

tered distribution of the seed sources tested, the analysis suggests that clinal variation exists within the tested samples. Apparently photoperiod, temperature regime, and precipitation are important selective pressures that molded white spruce as it extended its range after the termination of the last glaciation.

The data were also evaluated using Mahalanobis' "generalized distance function" (see Squillace (1966) for a discussion of this analysis and for additional references) and the principle component analysis. These tests support the clinal variation pattern—geographically close provenances are, on the basis of all measured characteristics, genetically closely related. Some seed sources appear to fall outside this general pattern, but with the limited sampling of the species it is not possible to decide whether or not these constitute separate ecotypes.

Height growth has been evaluated in extensive field tests in Canada and the United States. In 11 replicated outplantings in eastern and central Canada, provenances from the Great Lakes-St. Lawrence Forest Region all survived well but varied considerably in their rate of height growth. While local provenances exceeded the experimental mean by only 3 percent, the tallest provenances, mostly from the southern part of the range, exceeded the experimental mean by 22 percent and had large percentages of plants surviving. In Canada one race from near Peterborough, Ontario, (31, fig. 5) exceeded the plantation mean in all test

Table 2.—Summary of the analyses of variance of 36 characteristics measured on nursery grown white spruce representing 28 provenances from the entire range of the species<sup>1</sup>

	F value	Co-variance <sup>2</sup> significance		F value	Co-variance <sup>2</sup> significance
<i>Age 1 year</i>			<i>Age 4 years</i>		
Height in mm	11.06***		Height in inches	15.61**	
No. of branches	4.37**	**	Caliper of stem	30.75**	**
Color of needles	6.51**		No. of branches	4.35**	**
Time of bud formation	1.71*		Branch length	10.63**	*
Bud color	19.36**		Shape of bud	2.77**	
			Bud color	5.67**	
<i>Age 2 years</i>			Length of buds	15.95**	**
Height in mm	8.56**		Needle length	5.40**	**
No. side branches	9.54**	**	Cross section of needle	2.94**	
Branch length	7.99**	*	Stiffness of needles	2.55**	n.s.
Root length	2.39**	n.s.	Needle color	n.s.	
No. of side roots	2.76**	*	Needle curvature	2.42**	
Needle length (2)	7.31**	**	No. of stomata upper	2.72**	
Rows of stomata (3)	5.02**	n.s.	No. of stomata below	4.59**	**
Serrulation on needles (2)	2.52**		Serrulation on needles	6.08**	
Root dry weight	n.s.		Branch pubescence	8.05**	
Top dry weight	1.70*		Length of sterigmata	4.68**	**
Needle dry weight	1.70*		Secondary bud flushing	n.s.	
Stem dry weight	n.s.		Forking	3.78**	

<sup>1</sup> Data on file North Central Forest Experiment Station, Institute of Forest Genetics, Rhinelander, Wisconsin.

<sup>2</sup> Co-variables were heights at age 1, 2 and 4 respectively, co-variance analyses carried out for selected characteristics only.

<sup>3</sup> \*\* and \* significant at the 1 percent and 5 percent levels, respectively.

locations by an average of 17 percent (Teich, 1970b). Similar results were obtained with a Beachburg, Ontario, seed source (1663, fig. 5 and fig. 6) in the U.S.A. Furthermore, a 35-year-old test growing in northern Wisconsin that includes a seed source from the same region in southeastern Ontario supports the view that the juvenile height growth superiority of these two provenances will persist to or near maturity (Nienstaedt, 1969). These studies suggest that white spruce from the entire southeastern part of its range might yield excellent material for further tree improvement in the region described by the test plantings. A search for new high yielding provenances should include the entire region (fig. 5), but the search should be concentrated in the area between 72° and 85°W longitude and south of 48°N latitude (Nienstaedt, 1969).

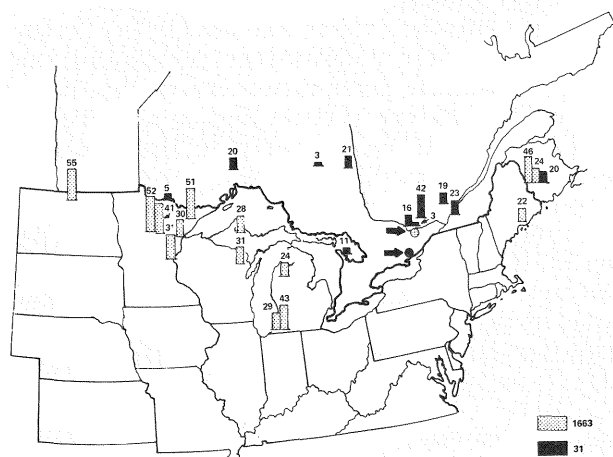


Figure 5.—Results with Beachburg and Peterborough provenances in 25 tests in the U.S.A. and Canada. The bars correspond to the approximate location of the test areas and show the percentage by which the respective sources exceed the plantation mean.

In replicated trials at Buckthorn and Aleza Lakes in the Prince George Forest District, British Columbia, a provenance from the southern part of the Columbia Forest Region was 30 percent taller than the experimental average at 4 years of age (Revel, 1969).

Wood density information is limited. Jones,<sup>7</sup> as reported by Holst (1960) in a study of 10 provenances and sampling only 5 trees per provenance, found the densest wood (sp. gr. 0.384) in a provenance from British Columbia and the lightest (sp. gr. 0.336) in a Quebec

source. The differences between individual trees were as great as the provenance differences. Holst (1960, 1962) concluded that, in terms of dry matter production per acre, growth rate is more important than wood density. Chang and Kennedy's (1967) study of growth rate and specific gravity of superior trees strongly supports this conclusion.

There is practically no information on variation in disease or insect susceptibility. Wright (1971) in a study of 24 provenances found one provenance (the border rows of unknown Michigan or Wisconsin origin) suffering heavy attack by a gall aphid. Preferential feeding by the yellow-headed spruce sawfly (*Pikonema alaskensis* Roh.) was observed on trees from 28 seed sources growing in northeastern Minnesota; scorings of the amounts of defoliation in the fall of 1968 and again in 1970 were significantly correlated  $r = 0.84$ .<sup>4</sup> The differences apparently are found only where insect infestations are light; no differences were found in another heavily infested Minnesota test of the same provenances.

Cell nuclear volume is larger in northern than in southern provenances, and possibly functions in cold resistance (Mergen and Thielges, 1967).

An increasing amount of evidence is accumulating which divides the species into two major populations—an eastern and a western. Wilkinson, Hanover, Wright, and Flake (1971) studied monoterpenes in cortical samples from 16 populations of white spruce growing together in a replicated test in southern Michigan. Four monoterpenes, beta-pinene, limonene, beta-phellandrene, and 3-carene, differed significantly among provenances. The most notable feature of the geographic variation pattern was the difference between eastern and western provenances. DNA content per cell varies within the species by a factor of 1.6. The number of samples in this study was also limited, but Miksche (1968) suggested that two distinct populations may exist. There is a direct relationship ( $r = 0.71$  significance is the 5 percent level) between latitude and cell DNA content in the west, while among eastern provenances the two characteristics are independent. Needle characteristics, such as color and length and other taxonomic characteristics, also show east-west variation patterns.<sup>4</sup> Clearly a division of white spruce into only two major populations is a gross over-simplification. On the other hand, such a major division corresponds to the refugia that have been described and to the suggested migration routes. Halliday and Brown (1943) postulated that one taxo-

<sup>7</sup> Jones, N. 1958. A specific gravity comparison of white spruce provenances on two sites with stem- and branch-wood relationships. M. Sc. F. Thesis, Univ. New Brunswick, Fredricton, N.B.

nominally recognized race (*P. glauca* var. *albertiana* (S. Brown) Sarg.) probably originated in the Yukon refugium and from there spread eastward to meet the more typical white spruce in the province of Manitoba. Löve (1959) has also argued that the Agassiz Lake system formed an effective barrier that the eastern flora was unable to cross. Löve, therefore, suggests a long-distance migration from a forest reserve in the west along drainage channels that preceded present day rivers such as the Assiniboine. If, indeed, the present day spruce populations have evolved from populations that

survived both the Illinoian and Wisconsin glacier in widely separated refugia, one would expect today's eastern and western populations to be genetically distinct with the line of demarcation between the two located at approximately 95°W. This is in fact close to the dividing line drawn by Wilkinson *et al.* (1971) and Miksche (1968).

Putative genetic adaptation to soil parent material has been studied by Farrar and Nicholson (1967) and Cunningham (1971). Contrasting seed sources from soils over granitic bedrock with provenances from soil derived from



Figure 6.—Beachburg, Ontario Provenance in Grand Rapids, Minnesota test. The provenances marked with white cardboard are from left to right: McNally Lake, Quebec (46°-32'N, 76°-30'W); Beachburg, Ontario (45°-40'N, 76°-51'W); Fort Albany, Ontario (52°15'N, 81°-40'W); Old Town, Maine (44°-50'N, 68°-38'W); the small plant in the left foreground is from Lake Melville, Labrador (53°-46'N, 60°-05'W). Planted May 1962 with 2-2 stock. Photo Nov. 1970.



limestone, Farrar and Nicholson (1967) compared growth in nutrient solutions of different  $\text{Ca}^{++}$  concentrations. There was some evidence for the existence of genetic differences between the two groups, but the study was unreplicated and the data included much unexplained variation. Cunningham's (1971) study involved two pH levels and three  $\text{Ca}^{++}$  concentrations, and the growth of the ten provenances resulted in significant seed source  $\times$   $\text{Ca}^{++}$  interaction. Trees from some seed sources grew well in terms of stem length at all levels of calcium, while others grew poorly at the highest (200 ppm) calcium level. Root lengths, and stem, and root weights were also studied and the results indicated that the type of growth variable examined influences the conclusions drawn regarding adaptation to particular levels of calcium nutrition. Cunningham found no association between progeny performance and soil pH or  $\text{Ca}^{++}$  of the parent habitats, and it was therefore not possible to identify pH or calcareous ecotypes. In a second test, the effect of variation in the total concentration of nutrients in solution was studied. Progeny stem length and foliar calcium were significantly correlated with several parental soil and foliar chemical elements, and was interpreted as evidence of genetic adaptation to soils high in nutrient availability.

Under laboratory conditions, temperature influences germination of different provenances differently (Roche, 1969b; Fraser, 1971). Fraser (1971) found that seed from northern sources germinated at temperatures as low as 7°C, while more southern provenances required at least 10°C to germinate. Optimum cardinal temperatures ranging from 13°C to 24°C, and upper cardinal temperatures ranging from about 29°C to 35°C were not clearly associated with latitude of seed source. Roche (1969b) found germination rate (adjusted for embryo development) at 25°C to be negatively correlated with latitude and the index of vegetative period, and positively correlated with altitude of seed source.

### Genetic Variation Within Provenances

Estimates of genetic variation within provenances have generally been obtained by studying variation of progenies resulting from wind-pollination in order to predict the potential genetic improvement from mass selection. In a study of Ontario stands, additive genetic standard deviations<sup>s</sup> were estimated to be about 8 percent of means of all progeny. An estimated

10 percent increase in rate of height growth would result from selecting the trees from the tallest 10 percent of the progenies. Leader number was also genetically controlled but variation in branch length was not (Holst and Teich, 1966, 1969). Jeffers (1969) found considerably more additive genetic variance for total height growth and rate of height growth during the fourth growing season in 4-year-old seedlings. Estimating genetic variance by the method used by Holst and Teich (1969), additive genetic standard deviations<sup>s</sup> were about 33 percent of means of all progeny. Furthermore in a Chalk River, Ontario, Study, additive genetic variance of height was greater at 11 years than at 19 years (Teich, 1970b).

Seedlings selected for superior growth when 4 years old in the nursery maintained their growth advantage for at least 7 years in the field and suffered less frost injury than slower growing seedlings. These results suggest an easy, reliable method of selection (King, Nienstaedt, and Macon, 1965).

The date of budbreak varies as much as 21 days (fig. 7) among trees in a stand; the factor is under strong genetic control and influences height growth and bud frost resistance. Nienstaedt and King (1969) found that in spite of the fact that late and early flushing trees had similar lengths of growing periods, the late flushing trees (grafted clones) were 42 percent

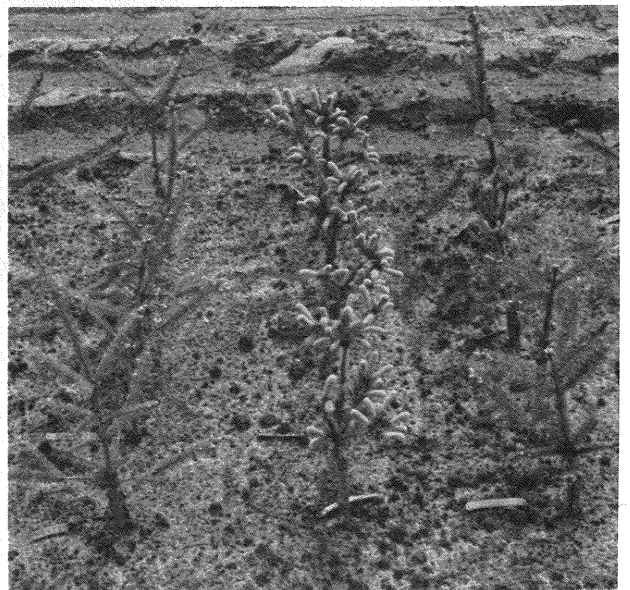


Figure 7.—Early white spruce clones in a nursery test with late flushing clones at Rhinelander, Wisconsin. Clones differ as much as 21 days in date of budbreak.

<sup>s</sup> Square root of the additive genetic variance.





Figure 8.—In the greenhouse and growth rooms, this white spruce progeny test yielded heritability estimates for the date of budbreak ranging from .28 to .70 depending on test conditions and method of computation. Photo August 1970.

taller, had 50 percent greater daily growth rates, and had only 16 percent as many frost injured buds. They estimated heritabilities in a study (fig. 8) of control-pollinated progenies and concluded that the risk of frost could be reduced by at least 40 percent in a climate similar to that of northeastern Wisconsin.

Pollen of different genotypes varies in sensitivity to gamma radiation. In a selfing study of three white spruce females, one tree had an  $LD_{50}^9$  of 4 kR and two others 5.7 kR and 10.7 kR respectively (Rudolph, 1969), while in another study Rudolph (1971b) found a range of  $LD_{50}$  exposures from 6.9 kR to 8.1 kR for three pollen parents when crossed with four other trees. In all cases, the endpoint used for evaluating the sensitivity was the percent germination of seed larger than 1 mm. Using other endpoints the  $LD_{50}$  exposure range was from 4 kR to 12 kR. Stimulatory effects at exposures below 3.0 kR also varied with genotype, and there appears to be an interaction in the stimulatory response

<sup>9</sup> Lethal dosage 50 percent. The dosage at which the response, such as survival or germination, is reduced to 50 percent of the response of the control.

between treatment and pollen and female parent (Rudolph, 1965, 1969, 1971b).

Although there is a wide variation in the total number of seeds and the number of filled seeds per cone within the individual clone (Rudolph, 1969, 1971b), fruitfulness undoubtedly is a characteristic under strong genetic control. On the average, the total number of seeds per cone, the number of filled seed per cone, and the total number of cones produced vary among clones (King, Jeffers, and Nienstaedt, 1970; Nienstaedt and Jeffers, 1970). Their data suggest that the ramets from the slower growing ortets were the most prolific cone producers. If these findings are substantiated, this relationship would be an important consideration in white spruce selection and seed orchard management.

Peroxidase and esterase isoenzymes have been studied in white spruce by Feret (1970). Half-sib, full-sib, and selfed progenies were compared on the basis of 10 peroxidase and 4 esterase isoenzymes isolated by means of disc electro-phoresis. Within the full-sib families, heterogeneity was less than in the case of open-pollinated families, and selfed families were, as expected, the least heterogeneous. The complement of peroxidase was family specific and segregation for peroxidase phenotypes was observed in all full-sib and in two of the three families derived from selfing, but a simple genetic model accounting for the segregation could not be established. Esterase profiles were also family specific and could be used to characterize each family. Feret concludes that there is a direct correspondence between the potential isoenzyme complement of an individual and its genotype; while the enzyme phenotype is the result of the isoenzyme potential modified by environmental factors, genotype-environment interactions, developmental factors, and allelic interactions. In spite of this, there was a highly significant correlation between indices of enzyme variation and family growth responses, suggesting that "the analysis of enzyme variation, as an indicator of within-family allelic heterogeneity, was useful as a predictor of family growth responses, and indicated that heterozygosity is an important determinant of height growth."

### Cytogenetics

*Picea glauca* has a diploid (2n) chromosome number of 24 (Santamour, 1960), but Winton (1964b) found about one out of 13,000 natural seedlings to be polyploid—mainly 4n but some

3n and 8n. The polyploids are stunted: their leaves are shorter and thicker than those of diploid plants and are swollen to roundness in cross section. In cultures of dividing callus cells from normal diploid tissue, a few cells

may be tetraploid and there are almost no aneuploids. Cultured tumor cells, however, contain from 3 to 70 chromosomes, with a higher proportion of the cells aneuploid (De Torok and White, 1960).

## IMPROVEMENT PROGRAMS

Potential benefits from the production and use of improved strains of white spruce exceed the required research and development costs (Carlisle and Teich, 1970). This is primarily due to the large amount of genetic variability, to the extensive area suitable for growing white spruce, and to the desirable qualities of the species to the wood-using industries. Of these factors, genetic variability and its exploitation are the concern of tree breeders. Several options are open to breeders in the methods of tree improvement: (1) selection of superior provenances, (2) hybridization of provenances, (3) selection of superior individuals within provenances for random or systematic crosses, and (4) species hybridization.

In the broad area from the Lake States through adjacent Ontario and east through parts of New England, Quebec, and New Brunswick, white spruce from the Lower Ottawa Valley and adjacent areas (Beachburg and Peterborough, fig. 2) probably will be the best choice of provenances on the basis of the available information. Planting these tested provenances should generally increase rate of height growth more than 15 percent over the indigenous provenance. Increases in growth rate of merchantable volume is expected to be considerably greater than 15 percent. This recommendation is based on relatively young tests and although major changes in the comparative growth rate of these seed sources are not expected as the tests grow older, we recommend that commercial plantings be established with mixed stock of the Ontario seed sources and a good local seed source. This procedure will reduce the risk of unexpected losses. Steps are now being taken to obtain the seed on a commercial scale.

Based on what we know, recommendations can be made for improvement programs based on the selection of superior individuals within provenances for random or systematic crosses. One large-scale developmental breeding program has been undertaken by the USDA Forest Service and exemplifies a recommended procedure. Three seed zones are delineated in Minne-

sota, Wisconsin, and Michigan. These zones are compromises between climatic and administrative considerations. Fifty phenotypes of superior vigor and good form have been selected within each seed zone. Forty grafted ramets of each clone have been planted according to a computerized planting scheme that assures maximum cross pollination (developed by Stairs, University of Wisconsin). The ramets are staggered 30 feet apart in rows spaced at 15 feet. The orchard will be rogued on the basis of half-sib and full-sib progeny tests.<sup>10</sup> The evaluation will be on the basis of vigor, the time of flushing (a factor that also should be considered in future phenotypic selections), form, and secondary factors such as pest resistance and quality of wood. A first-generation seed orchard of this type should be followed by future orchards built of progeny tested ortets of proven genetic quality.

Another type of orchard is also being developed in Canada and the United States. It combines provenance and individual phenotype selection. The selections are made in the native stands or existing tests of the Beachburg and Peterborough provenances from southeastern Ontario. Although smaller in size, the orchards will be of the design already described.

Specific recommendations for the maintenance of seed orchards are not available. Presumably, it is advantageous to control weed competition by clean cultivation or with acceptable herbicides. After the trees are 3 to 4 feet tall, mowing the ground cover may be adequate. A relatively high level of soil fertility probably should be maintained, but we don't know whether or not seed production can be stimulated through fertilization. It would be desirable to maintain the crowns low for easy cone picking, but this would require some type of pruning that could have adverse effects on seed yield. Pruning cannot be recommended with the available information.

Genetic improvement by hybridization between species has not yet been evaluated with

<sup>10</sup> Miller, R. G. Report on file, Nicolet National Forest, Rhinelander, Wisconsin.

certainty. Low seed yields in most interspecific hybrids and scarcity of adapted parent material of exotics are potential problems. With the possible exceptions of *P. omorika* x *P. glauca*, *P. schrenkiana* x *P. glauca*, *P. glauca* x *P. jezoensis*, *P. glauca* x *P. engelmannii*, and *P. glauca* x *P. sitchensis*, species hybridization should be considered a research responsibility. The potential gain from species hybridization is great, but an organization basing a tree improvement program on any of the hybrids we have listed should be willing to assume risk of failure.

If a hybridization program between white spruce and exotic species is chosen, the following plan is recommended:

1. Select the best adapted parent material, i.e.:
  - (a) Selected white spruce of proven genetic quality if possible
  - (b) At least a dozen individuals of the exotic that are adapted to the environment in which the hybrid will be used.
2. Through small-scale test crosses, select the most highly cross-compatible parent combinations.
3. If the selections are phenologically synchronized, grafted seed orchards can be

used. Their design will depend on the ease with which the hybrids can be distinguished from the two parent species.

- (a) If they are easily identified, the orchard can consist of several clones of each species. The total harvest would be seeded in the nursery; the hybrids would be sorted out on the grading tables.
  - (b) If the hybrids are difficult to identify, the orchards will involve only a single clone of each parent so that only hybrid seed will be produced.
4. If the flowering of the parent selections are not synchronized, methods of large-scale artificial pollination would have to be developed. It should be mentioned that reciprocal crosses can be so different that only the cross in one direction will be of value.

The potential gain from a provenance hybridization program should be great, but much additional research will be needed before the potential can be used in a tree improvement program. There is, as yet, no reason to incorporate polyploidy into breeding programs because polyploids in themselves have no apparent advantage, and their use as a hybridization bridge with other species is not required.

## RESEARCH NEEDS

Gaps in our present understanding of the genetics of white spruce and some shortcomings of past research have been mentioned. Some research needs are discussed below.

*Provenance research* has been based on too few samples; most samples have been from southern Ontario and Quebec, while the vast western, northern, and extreme southern populations have only been represented by a few samples. A new study should be started as soon as possible in order to meet the following objectives:

1. Adequately describe the population structure of the species.
2. Identify additional promising provenances for planting within the commercial range of the species.
3. Provide material for provenance hybridization studies and for further breeding.

The study probably would require a minimum of 150 provenances and sampling could be of varied intensity over the range of the species, with the greatest number of samples concen-

trated within the main commercial range. We suggest that basic studies of population structure and genecology and similar studies that require the total number of samples be conducted as short-term studies (4-5 years) in the nursery. Field testing should be limited to a selected number of provenances and the complement of provenance can be varied depending on the test environment.

*Provenance hybridization* is another high priority area of research. Only the earliest tests, which included very few provenances, are now flowering; they are not sufficient for hybridization studies. The studies established in the early 50's—mostly Ontario and Quebec provenances—are beginning to produce cones and can answer a limited number of questions. More detailed studies, however, will have to await the sexual maturity of trees in rangewide studies established more recently. Studies should seek answers to basic questions: What are the relative merits of "wide" versus "narrow" crosses? How do hybrids between geographically remote

but climatically similar provenances compare in growth rate and reaction range to hybrids between climatically dissimilar provenances? Is it possible to predict the reaction range of provenance hybrids?

Biometric data are needed in order to simplify testing and reducing costs of tree improvement. We still need reliable correlations between juvenile and mature characteristics. The number of measurements can be reduced and selection simplified if pertinent character correlations can be determined; this can be particularly important when breeding for insect or disease resistance. Variants with unique phenological growth patterns, needle or branch morphology, rate of resin flow, or terpene composition may be resistant. With the correlation established, selections can be made in areas of low infestation and progenies evaluated without going through difficult inoculation procedures.

Genetic parameters such as estimates of the number of genes controlling commercially important characteristics and general estimates of the heritability of such characteristics, are needed.

*Components of yield and pest and disease resistance* are not now known. Efficient use of solar energy as determined by needle characteristics and crown structure, photosynthetic efficiency, distribution of photosynthetic products to stem or crown, use of available and/or supplied fertilizer and water, and the phenology of growth are some of the characteristics of the individual tree that determine per-acre yields. Now we evaluate their total effect in terms of height and diameter growth or dry matter production per acre. If the contribution of each factor and its genetic control could be determined, it might be possible to increase growth through breeding for combinations of characters beyond what can be achieved through the systematic crosses that now are in use. Much white spruce material is now growing in breeding collections in Canada and the U.S.A. that could be profitably studied from this point of view.

Resistance breeding has not been a major area of white spruce research but some smaller studies of sawfly and gall aphid resistance are on the way. These and future studies of other pests and diseases should from the beginning attempt to determine the components of resistance. This could simplify selection procedures and breeding.

*Seed orchard designs* are largely arbitrary. We do know how to place the clones relative to each other in order to achieve maximum cross-fertilization; we are beginning to get information on the potential yield of seed. We do not, however, have an answer to the basic question: What is the optimum number of clones or families of seedlings to be included in a seed orchard?

Although future pulp production will require more intense cultural practices and more specific site selection, tree planting probably will continue to be done on a wider variety of site than we encounter in agriculture. Products of tree improvement must, therefore, be endowed with a greater reaction range than is required, for example, for hybrid corn. How do we achieve this goal? By increasing the number of parent clones all selected within the same provenance or by including selections from several different provenances?

Other orchard designs may also be considered. Many selfed families are available; would it be possible to obtain heterotic new strains in orchards based on two or more clones of inbred material?

Although most of the research needed to assure better yields of seed, ease of harvesting, and so on fall outside the field of genetics, one area has possible genetic implications. It has been suggested that better seed quality and greater yields (?) might be achieved if orchards are established in the warmer sections in the southernmost parts of the species range. This raises the still unsettled question of preconditioning (Rowe, 1964) and possible environmental effects on nuclear and extra-nuclear DNA. These are questions that deserve attention and could be studied in already established provenance tests, particularly where the same test is established over a considerable north-south gradient.

*Species hybridization* research probably should be considered lower priority than the research suggested above, yet much basic information relating to the early evolution of conifers could be derived from phylogenical studies of *Picea*. Considering the North American species, it should be particularly interesting to attempt to test the working hypothesis presented in this review. Cross-compatibility should be determined and fossil records reviewed.

Existing spruce material from continental Asia is extremely limited and not well suited for crossability studies. If it becomes possible

to obtain good provenance collections from China, the establishment of this material should be considered high priority. In the meantime, studies of crossability can probably best be limited to species that are well represented in collections in Canada and the United States.

*Intraspecific and interspecific studies of DNA, isoenzymes, and monoterpenes* are more basic research areas that could lead to new methods that would simplify breeding.

It has, for example, been suggested that DNA content and isoenzyme heterogeneity may relate to vigor and could serve as predictors. Studies of DNA-DNA hybridization may be

used as predictors of crossability and could lead to simplified improvement through species hybridization. All three factors would aid in the understanding of the population structures in white spruce and of introgressive hybridization.

Many other basic problems need study—*maternal inheritance*, the possible development of *monoploids*, *endopolyploidy*, and *DNA base composition*—just to mention a few. Suffice to say, any comprehensive program of white spruce genetics should use existing plant material to study these and similar problems if staffing, facilities, and budgets permit.

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